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The comparative effects of habitat complexity on faunal assemblages of northern temperate artificial and natural reefs

W. R. Hunter and M. D. J. Sayer

Several north temperate marine species were recorded on subtidal hard-substratum reef sites selected to produce a gradient of structural complexity. The study employed an established SCUBA-based census method, the belt transect. The three types of reef examined, with a measured gradient of increasing structural complexity, were natural rocky reef, artificial reef constructed of solid concrete blocks, and artificial reef made of concrete blocks with voids. Surveys were undertaken monthly over a calendar year using randomly placed fixed rope transects. For a number of conspicuous species of fish and invertebrates, significant differences were found between the levels of habitat complexity and abundance. Overall abundance for many of the species examined was 2–3 times higher on the complex artificial habitats than on simple artificial or natural reef habitats. Perhaps the enhanced habitat availability produced by the increased structural complexity delivered through specifically designed artificial reefs has the potential to augment faunal abundance while promoting species diversity.

Keywords: **a**bundance, activity indices, artificial reef, faunal assemblages, habitat complexity, SCUBA, visual census.

Introduction

Artificial reefs have been employed worldwide for a variety of primary purposes. Examples are to support fisheries protection, to promote pollution mitigation, and to enhance recreational opportunities (Jensen *et al.*, 2000). Probably their most important uses, however, are as tools to address declines in commercial fisheries or in enhancing their recovery (Baxter, 2000; Sayer, 2001). More than 30 countries have deployed artificial reefs within their territorial waters with a stated primary purpose that is in some way related to fisheries (Jensen, 2002; Seaman, 2002). When used in combination with marine protected areas (MPAs), artificial reefs demonstrate an enhanced potential to restore depleted fish stocks (Pitcher *et al.*, 2002). However, their use in that context remains controversial, principally because of the debate surrounding whether such reefs simply attract and concentrate fish, which could promote localized overexploitation, or if there is any net productivity in the fishery (Brickhill *et al*., 2005).

Several studies have reported positive impacts of increasing the complexity of available habitat on fish abundance (e.g. Fujita *et al*., 1996; Charbonnel, *et al*., 2002), species richness (e.g. Fabi and Fiorentini, 1994; Charbonnel *et al*., 2002; Gratwicke and Speight, 2005), and species diversity (e.g. Roberts and Ormond, 1987; Fabi and Fiorentini, 1994). All these studies suggest that the increased variation in habitat type and size afforded by artificial reefs removes some environmental or ontogenic bottlenecks that may affect any net gains in productivity of commercially important fish species.

Numerous researchers have attempted to demonstrate the effects of anthropogenic manipulation of habitat complexity, but much of the research has been compromised by associated legal or financial constraints that limit the ability to develop formal hypothesis testing (Bortone, 2006), provide acceptable levels of replication (Kock, 1982; Fabi and Fiorentini, 1994; Fujita *et al*., 1996; Charbonnel *et al*., 2002), and/or avoid pseudoreplication (Kock, 1982; Bortone *et al*., 1994; Jensen *et al*., 1994). Moreover, most studies carried out on artificial reefs have focused solely on a single assemblage type. For example, Fabi and Fiorentini (1994); Charbonnel *et al*. (2002), and Gratwicke and Speight (2005) concentrated on fish alone, and Badalmenti *et al*. (2002) examined the effects on molluscs only.

Past research on artificial reefs has tended to be based in subtropical or tropical waters (e.g. Seaman 2002; Gratwicke and Speight 2005). There are only a few examples of artificial reef research being undertaken in northern temperate waters (e.g. Grant *et al*., 1982; Jensen *et al*., 1994; Wilhelmsson *et al*., 2006). However, although not tested, it may be expected that the biotic support afforded by reefs would be evident at similar trophic levels, irrespective of geographical location.

The aim of the current study is to compare the composition and diversity of animal assemblages measured on artificial and natural reefs that present a gradient in habitat complexity. The comparison is based on examinations of common reef-inhabiting species, such as the fish from the family Labridae and the portunid crab *Necora puber*. Facultative users of reef habitats, such as juvenile cod (*Gadus morhua*), have been observed previously to survive better when living in more structurally complex habitats (Tupper and Boutillier, 1995). A similar observation has been reported for the highly nomadic crab *Cancer pagurus* (Bennett and Brown, 1983).

Methods

Study site

The Loch Linnhe Artificial Reef (LLAR) is a multi-modular artificial reef complex constructed over 146 ha in Loch Linnhe, on a mixed sand/mud seabed on the west coast of Scotland. Construction of the reef commenced in 2002, and all reef modules used in this study were deployed between 2003 and 2004. The part of the LLAR used in the present study consisted of 30 reef modules clustered into groups of six, lying within a depth range of 10–20 m. Each reef module was constructed as a conical pile of >4000 concrete blocks, each 20 × 20 × 40 cm (Wilding *et al*., 2007). Within each reef group of six modules, three were constructed exclusively from "simple" blocks, which are solid, and three were constructed exclusively from "complex" blocks, which are each perforated by two cuboidal holes.

Reef module designations were assigned by the project management committee of the LLAR, providing information on the position of each reef module. Each of the five groups of artificial reef modules was assigned a letter (A–E) designating its position in the overall reef complex. Within each reef group, the six individual modules were designated with a number and letter code which indicated whether a reef was constructed from complex blocks, i.e. 1c–3c, or simple blocks, i.e. 1s–3s.

Six artificial reef modules were selected from the LLAR to act as artificial reef stations for the experiment. Three complex and three simple artificial reef stations were selected at random from the 30 reef modules available. Randomization was at two levels, initially through selection of a reef group, and then through selection of one complex and one simple artificial reef module within each reef group. The complex artificial reef modules selected were designated B2c (56°32.113'N 5°27.330'W), C2c (56°32.119'N 5°27.103'W), and D1c (56°32.222'N 5°26.933'W). The simple artificial reef modules selected were designated B1s (56°32.102'N 5°27.373'W), C2s (56°32.099'N 5°27.076'W), and D2s (56°32.224'N 5°26.880'W).

Three natural reef stations were selected in the Lynn of Lorn area; Loch Linnhe is a component part of the Lynn of Lorn system. All natural reef stations were selected to be in a similar depth range to the LLAR stations and were surrounded by a sand/mud seafloor similar to that observed at the LLAR site. These stations were located at the Creag Isles (CI; 56°28.655'N 5°30.950'W), Eilean Mhor (EM; 56°27.348'N 5°26.034'W), and Saulmore Point (SP; 56°27.245'N 5°24.810'W).

At the same sites listed above, a previous study had quantified habitat complexity (Wilding *et al*., 2007), using fractal geometry to compare the size of the available spaces within a reef in which an organism may take refuge. That study demonstrated that the complex artificial reef modules provided a greater level of habitat complexity than the simple artificial reef modules or than a number of the surrounding natural reef sites. The greatest difference in complexity was in the space size range 253–511 mm.

Sampling technique

Sampling consisted of a matrix of underwater visual censuses carried out by SCUBA divers using the belt transect technique of Brock (1954). The belt transect was chosen for this work because it was shown by Kimmel (1985) to provide a high level of accuracy in assessing fish abundance.

Two permanent belt transects were deployed at random at every natural and artificial reef station, in depths of 10–18 m. The transects were marked using a rectangular boundary constructed from 12-mm leaded rope with 15-mm plastic pipe at each end. Each transect was 6 m long and 1.5 m wide, and was surveyed using SCUBA at a speed of 1.5 m^2 min^{-1} to an estimated height of 1 m above the reef. Transect area and survey speed parameters were consistent with those considered optimum for conducting visual surveys of marine fauna in north temperate conditions (Sayer and Poonian, 2007). The surveys concentrated on recording 17 conspicuous species of fish and mobile invertebrates (Table 1). Of these 17, seven species of actual or potential commercial importance were selected for examination within the study. These were the labrids *Crenilabrus melops* and *Ctenolabrus exoletus*, which have previously been examined tentatively as a potential cleaner fish in aquaculture (Sayer, 1996), juvenile gadoids *Gadus morhua* and *Pollachius pollachius*, and the crustaceans *Cancer pagurus*, *Necora puber*, and *Munida rugosa*.

Sampling stations were visited monthly between August 2005 and June 2006; individuals of each target group were recorded per unit area (per m^2). Nominal seasons were defined based on water temperature (Table 2), and the monthly abundance data for each station were then used to calculate seasonal averages.

Data analysis

For each of the four nominal seasons, the total animal abundance for each station was calculated by aggregating the census data for all species. The total animal abundance, and the abundance of the seven species selected as being of commercial relevance, were compared between the three site types using one-way analysis of variance (ANOVA). The data did not exhibit equal variance when analysed using Levene's test with a rejection value of $p > 0.05$ (Underwood, 1997). Data were re-sampled using the bootstrap methods of Diaconis and Efron (1983), as applied by Sayer and Poonian (2007) for underwater censuses. This methodology supported parametric statistical testing, so overcame the requirement to sacrifice sensitivity by applying non-parametric tests (Thomas and Juanes, 1996). It also satisfies the assumptions of homogenous variance that may have been necessary for untransformed data (Underwood, 1997).

Bootstrap re-sampling was carried out based upon units of 500 re-samples using the SIMSTAT statistical software. The bootstrapped data were used to test for differences between site types, for each species, using one-way ANOVA. If a significant difference was detected, a *post hoc* Fisher's pairwise test was used to determine the source of the difference, with a significance level of $p = 0.05$.

Multivariate examination of the seasonal data was carried out using the PRIMER statistical package (Clarke and Warwick, 2001). All data were transformed by $\log(x+1)$ and converted to a triangular similarity matrix using the Bray–Curtis similarity coefficient. Subsequent cluster analysis gave scaled, graphic representations of the differences between the four site types. Additionally, PRIMER was used to calculate Shannon–Weiner diversity indices (H') for each reef station using $\log(x+1)$-transformed monthly data. These monthly diversity indices were assigned to their corresponding seasonal regimes and tested on a seasonal basis for any difference in the level of diversity at each of the three habitat types under investigation. Following Levene's test for normality, analysis was carried out on the diversity indices using one-way ANOVA with Fisher's pairwise comparisons. The data for summer, autumn, and spring required no transformation, but winter data required transformation using the bootstrap method outlined above.

The following assumptions were made during the course of the study to support the level and type of analysis. First, it was assumed that any influences on abundance counts caused by

the presence of divers were consistent (Buxton and Smale, 1989; Sayer and Poonian, 2007). Second, it was assumed that the size of the belt transects mitigated against any changes in the detectability of target species caused by variations in water clarity (Sayer and Poonian, 2007). Third, it was assumed that any variability between sites was controlled by adequate and randomized replication.

Results

In all, 234 surveys were carried out during the study, with two transects being surveyed monthly at each station. These raw data were used to generate bootstrapped mean and confidence intervals for each site type during the four seasons. The data were then used to test for differences in animal abundance between experimental stations at the complex artificial reef, simple artificial reef, and natural reef sites, using analysis of variance (Table 3). Although many of the results and comparisons were true abundance data, some of the observations would have been influenced by seasonal activity patterns (Sayer and Poonian, 2007).

Variations in the total animal abundance and diversity are displayed graphically in Figure 1; there was no significant difference in animal abundance on the complex artificial reef stations between summer, autumn, and winter ($p > 0.05$). During spring, however, there was a significant difference in total abundance between sites ($p < 0.05$); Fisher's pairwise tests identified significantly greater animal abundance on both the complex artificial reef and natural reef stations than on the simple artificial reef stations ($p < 0.05$ in all cases). However, no significant differences were detected between the complex artificial reef and natural reef stations ($p > 0.05$).

There were low levels of variation in diversity of animal assemblages between site types, with no significant differences evident in either summer or autumn ($p > 0.05$ in both cases; Figure 1). During winter and spring, however, ANOVA showed a significant difference in diversity between site types, and *post hoc* testing identified the complex artificial reefs stations as exhibiting significantly greater diversity than the simple artificial or natural reef stations ($p < 0.05$).

The relative abundance of fish species tended to be low at all site types, across the four seasons (Figure 2). During summer, the relative abundance of the corkwing wrasse (*Crenilabrus melops*) was significantly greater at the complex artificial reef stations than at either the simple artificial or natural reef stations, as identified by ANOVA ($p < 0.05$) and *post hoc* testing ($p < 0.05$; Figure 2a). In autumn there were no significant differences in the abundance of *C. melops* between habitat types ($p > 0.05$), and too few were seen during winter and spring to make valid comparisons (Figure 2a).

Rock cook (*Ctenolabrus exoletus*) were observed only at the complex and simple artificial reef stations during summer; relative abundance at both sites was ~0.20 m^{-2}, with no significant differences between the two sites (Figure 2b). During autumn the relative abundance of *C. exoletus* increased at all sites, with a significant difference in relative abundance between site types ($p < 0.01$); *post hoc* testing demonstrated abundance at the complex artificial reef stations to be significantly greater than at the other two types of site ($p < 0.05$; Figure 2b). Additionally, the relative abundance of rock cook on simple artificial reef stations was significantly greater than on natural reefs ($p < 0.05$). The abundance of rock cook in winter and spring was too low to make comparisons.

The relative abundance of juvenile gadoids was low at all site types for all four seasons, with no significant differences between habitat type ($p > 0.05$ in all cases; Figures 2c and d). In the case of cod, abundance was greatest in summer on the complex reefs, but did not exceed 0.10 m^{-2} at either the complex or simple artificial reef stations and was zero at natural reef stations (Figure 2c). Similarly, the relative abundance values of pollack did not exceed 0.30 m^{-2} at any site. However, great variability meant that, although more juvenile pollack were recorded at the complex artificial reef stations, any differences in abundance between habitat types were not significant during summer and autumn.

The crab *Cancer pagurus* was observed at low levels of abundance at all stations during summer and autumn, with abundance not exceeding 0.10 m^{-2} (Figure 3a). During winter, however, relative abundance on the complex artificial reef stations was 0.14 m^{-2}, significantly greater than at the other two habitat types (analysis of variance and Fisher's pairwise analysis; $p < 0.05$ in each case). During spring, there was no siginificant difference in *C. pagurus* level between the three habitat types (Figure 3a; $p > 0.05$ in each case).

Relative abundance of the crab *Necora puber* was greater than *C. pagurus* at the complex artificial reef stations, across all four seasons, ranging from 0.27 m^{-2} in summer to a peak of 0.46 m^{-2} during winter (Figure 3b). *N. puber* was also present on both the simple artificial and natural reef stations during all four seasons. There were significant differences between abundance per habitat type in all seasons (ANOVA; summer $p < 0.05$; autumn $p < 0.05$; winter $p < 0.01$; spring $p < 0.001$). For summer, a *post hoc* Fisher's pairwise comparison revealed only that there were significantly more *N. puber* on artificial reefs than on natural ones (Figure 3b; $p < 0.05$). However, in autumn, winter, and spring, *N. puber* abundance was significantly greater at the complex artificial stations than either simple artificial reef or natural reef stations ($p < 0.05$ in all cases).

Cluster analysis examined the level of similarity between all experimental stations, based on Bray–Curtis similarity indices (following Clarke and Warwick, 2001). During summer, all animal assemblages observed on complex and simple artificial reef stations could be grouped together with a similarity level of 60% (Figure 4a). However, no distinct partition could be drawn between complex and simple artificial reef assemblages. The natural reef assemblages were more variable overall, with the animal assemblages observed only exhibiting similarity of 25–35%.

In autumn, there was a greater extent of partitioning between assemblages observed at all stations, with the three complex stations sharing a similarity of 60%, and the simple artificial and natural reef stations showing a similarity of ~20% (Figure 4b). During winter, the similarity between the complex artificial reef station assemblages lay between 65 and 70%. The similarity between the assemblages on simple artificial reef stations was just over 60%, and at the natural reef stations was ~25% (Figure 4c). The animal assemblage similarity levels observed during spring were similar to those described in winter (Figure 4d). Overall Bray–Curtis similarity indices showed the animal assemblages on the complex artificial reefs to exhibit the highest levels of similarity in structure between reef stations; the natural reef assemblages exhibited the most variable structure between reef stations.

Discussion

The results of this study indicate positive relationships between levels of habitat complexity and abundance for some common temperate species. For all the monitored assemblage, relative abundance and diversity differed little with habitat type. However, when examined individually, some species tended to be more abundant on the complex artificial reef stations than on the other two types of reef, at least for the season's data analysed. Hence, the results of the present study agree with those of earlier studies that indicated positive relationships between increasing habitat complexity and numbers of fish (Fujita *et al*., 1996; Tupper and Boutilier, 1997; Charbonnel *et al*., 2002; Gratwicke and Speight, 2005), levels of species richness (Fabi and Fiorentini, 1994; Charbonnel *et al*., 2002; Gratwicke and Speight, 2005), and increases in species diversity (Roberts and Ormond, 1987; Fabi and Fiorentini, 1994).

The structure and execution of any study based on mainly mobile rocky subtidal macrofauna has to contend with numerous challenges. Although numerous studies have employed SCUBA divers to conduct census-based studies on these types of habitat (Sayer, 2007), many have been shown to over- and/or underestimate animal abundances. Much of the census variability is related to the behaviour of the target animal (e.g. attraction vs. repulsion; cryptic vs. obvious; reviewed by Sayer and Poonian, 2007). Abundance data collected in the present study were derived only from census observations standardized to optimum survey practice suggested for mobile macrofauna in north temperate waters (Sayer and Poonian, 2007). Therefore, although behavioural, ontogenic, and environmental factors can make

assessing macrofaunal abundances difficult (Magill and Sayer, 2002), and there are uncontrollable influences caused inevitably by the presence of the observer (Nash *et al*., 1984), standardization of census techniques, irrespective of site or habitat, should eradicate most inconsistencies so that any differences in abundances should be genuine (Sayer and Poonian, 2007).

The results of this study provide some indication of the effects of habitat complexity at a community scale by examining a sample of both the fish and invertebrate assemblage. Habitat complexity is greater on the complex artificial reefs of the LLAR than on the other site types (Wilding *et al.*, 2007). This study showed biotic diversity to be similar during summer and autumn, when animal activity was likely to be greatest. During winter and spring, however, the complex artificial reef habitat supported greater diversity, despite relatively little change in animal abundance. When examined individually, the fish species were most abundant in summer and autumn. In most cases, these peaks in abundance may be caused by behavioural or ontogenetic responses of temperate-water fish to seasonal variations in water temperature, eliciting some form of seasonal migration (Sayer *et al*., 1996). However, it is also possible that, for some fish species (especially the wrasses), there is a direct link between recorded abundance and seasonal activity levels, so the perceived lower numbers may primarily be caused by hypometabolic crypsis (Sayer *et al.,* 1994; Sayer and Davenport, 1996).

Few studies have examined the relationship between habitat complexity and the numbers of invertebrates. A study related to this one compared the epifaunal communities on the LLAR with surrounding natural reefs (Beaumont, 2006), employing increased grazing pressures as proxy evidence of higher abundances of grazers, such as sea urchins and starfish, on artificial reefs. The present study measured the relative abundance of two commercially important crabs, *Cancer pagurus* and *Necora puber*. In both cases, abundance was greater at the complex artificial reef station during one or more seasons. This is of particular interest in *Cancer pagurus* because of its nomadic behaviour (Bennett and Brown, 1983). Female *Cancer pagurus* require soft substratum during autumn for reproduction (Edwards, 1979), and shelter for the rest of the year (Howard, 1982). This already documented behaviour correlates with observations from the present study during winter and spring, when the crabs were observed to maximize their utilization of the increased shelter volume offered by the complex artificial reefs. In the case of *Necora puber*, relative abundance was 2–3 times higher at the complex artificial stations than at simple artificial and natural reef stations, across all four seasons. Therefore, that species clearly thrives in the habitat provided by the complex reef modules of the LLAR. However, the present study was unable to account for the residence time of either of these species at the experimental stations, or of how this may change with season.

Results from cluster analysis show that the artificial reef stations tended to group together with high levels of similarity. Most notably, high levels of similarity between complex artificial reef stations combine with the significantly greater diversity and faunal abundance at those stations to demonstrate greater stability in community structure. Hence, faunal assemblages of great abundance and diversity occur more predictably in habitats of greater complexity. Higher species diversity in communities may promote more complex foodwebs composed mostly of long trophic loops, dominated by weak interactions that are less susceptible to chaotic dynamics (McCann *et al.*, 1998; Neutel *et al.*, 2002). The reverse may also be true, communities with low species diversity promoting the dominance of a few strong interactions, resulting in reduced stability (McCann *et al.*, 1998). However, community resilience will increase as trophic interactions become weakened with the decreased predator efficiencies caused by increased structural complexity (Diehl, 1992; Grabowski, 2003). Our study has demonstrated positive relationships between habitat complexity and the abundance of commercially important fish and crabs. Habitat complexity also strongly influenced faunal abundance and diversity, providing support for links between habitat complexity and ecosystem function.

In conclusion, the results of our work have demonstrated that artificial structures deployed in northern temperate waters can support animal assemblages that are at least equal in terms of abundance and diversity to natural reefs. Increasing the habitat complexity

afforded by artificial structures may increase faunal diversity and abundance above levels supported by natural reefs. Our results lends weight to the hypothesis that artificial structures can protect, enhance and augment populations of some commercially important species (Sayer, 2001) by supporting similar or higher abundances than those found on comparable natural reefs. However, the scales and costs of the interventions required to produce net positive benefits remain to be quantified (Sayer *et al*., 2005).

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Table 1. List of organisms and their ontogenic stages used in the present study. The nomenclature follows Wheeler (1992) and Wheeler *et al*. (2004).

Common name	Scientific name	Authority	Age class
Corkwing wrasse	*Crenilabrus melops*	Linnaeus	Adult
Rock cook	*Centrolabrus exoletus*	Linnaeus	Adult
Goldsinny	*Centrolabrus rupestris*	Linnaeus	Adult
Ballan wrasse	*Labrus bergylta*	Ascanius	Adult
Cuckoo wrasse	*Labrus mixtus*	Linnaeus	Adult
Cod	*Gadus morhua*	Linnaeus	Juvenile
Pollack	*Pollachius pollachius*	Linnaeus	Juvenile
Saithe/coley	*Pollachius virens*	Linnaeus	Juvenile
Leopard spotted goby	*Thorogobius ephippiatus*	Lowe	Adult
Brown crab	*Cancer pagurus*	Linnaeus	Adult
Velvet swimming crab	*Necora puber*	Linnaeus	Adult
Shore crab	*Carcinus maenas*	Linnaeus	Adult
European lobster	*Homarus gammarus*	Linnaeus	Adult
Squat lobster	*Munida rugosa*	Fabricius	Adult
Edible sea urchin	*Echinus esculentus*	Linnaeus	Adult
Common starfish	*Asterias rubens*	Linnaeus	Adult

Table 2.Table showing the seasonal regimes imposed upon the data, and the mean seawater temperature recorded for each season.

Season	Months	Mean temperature (^{o}C)	s.e. of the mean
Summer	August–October 2005	13.4	0.1
Autumn	November–December 2005	11.4	0.1
Winter	January–March 2006	7.6	0.1
Spring	April–June 2006	10.2	0.3

Table 3. Summary of the ANOVA results, comparing animal abundance and diversity between complex artificial, simple artificial, and natural reef sites, across four seasonal regimes.

Species	Summer	Autumn	Winter	Spring
C. melops	*(d.f. 2; F = 6.87)	n/s	n/s	n/s
C. exoletus	n/s	**(d.f. 2; F = 23.21)	n/s	n/s
G. morhua	n/s	n/s	n/s	n/s
P. pollachius	n/s	n/s	n/s	n/s
C. pagurus	n/s	n/s	*(d.f. 2; F = 6.79)	n/s
N. puber	*(d.f. 2; F = 7.17)	*(d.f. 2; F = 5.53)	**(d.f. 2; F = 14.22)	***(d.f. 2; F = 25.22)
Total abundance	n/s	n/s	n/s	*(d.f. 2; F = 9.52)
Diversity	n/s	n/s	*(d.f. 2; F = 10.25)	***(d.f. 2; F = 9.95)

n/s not significant ($p > 0.05$); * significant at 0.05; ** significant at 0.01; *** significant at 0.001.

Figure 1. Graphs showing the mean and 95% confidence intervals for (a) the relative abundance of all fauna (open bars; per m^2) and diversity (shaded bars; *H'*), over the four seasonal regimes of summer, autumn, winter, and spring.

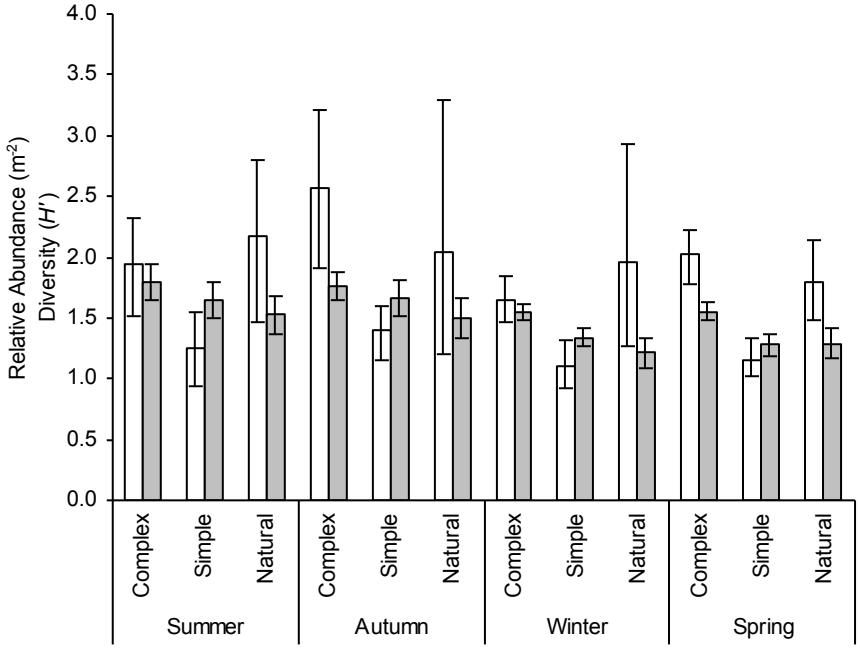
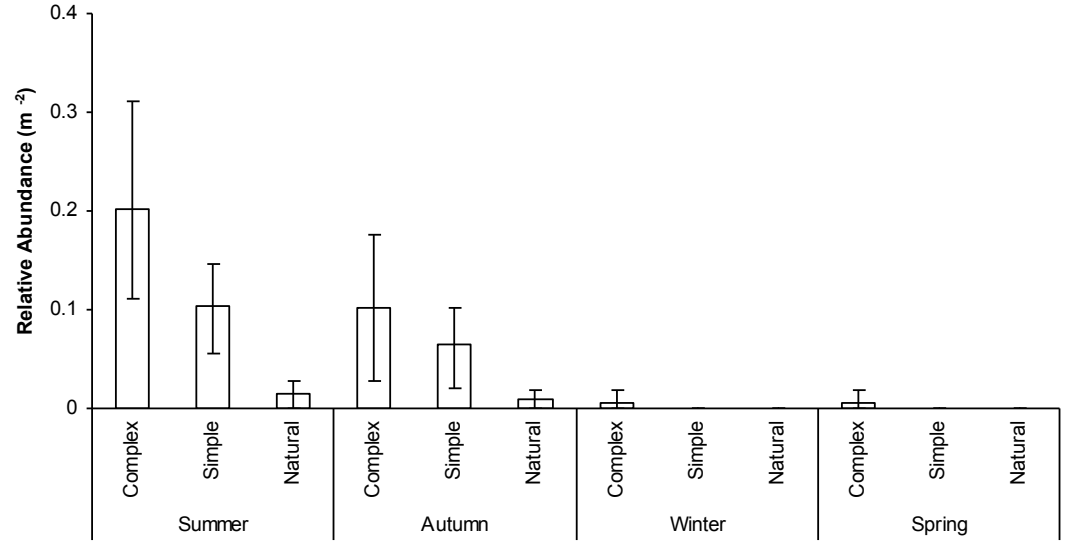


Figure 2. Mean relative abundance (per m^2) and 95% confidence intervals of the fish species (a) *Crenilabrus melops*, (b) *Ctenolabrus exoletus*, (c) *Gadus morhua*, and (d) *Pollachius pollachius*, over the four seasonal regimes of summer, autumn, winter, and spring.

(a)



(b)

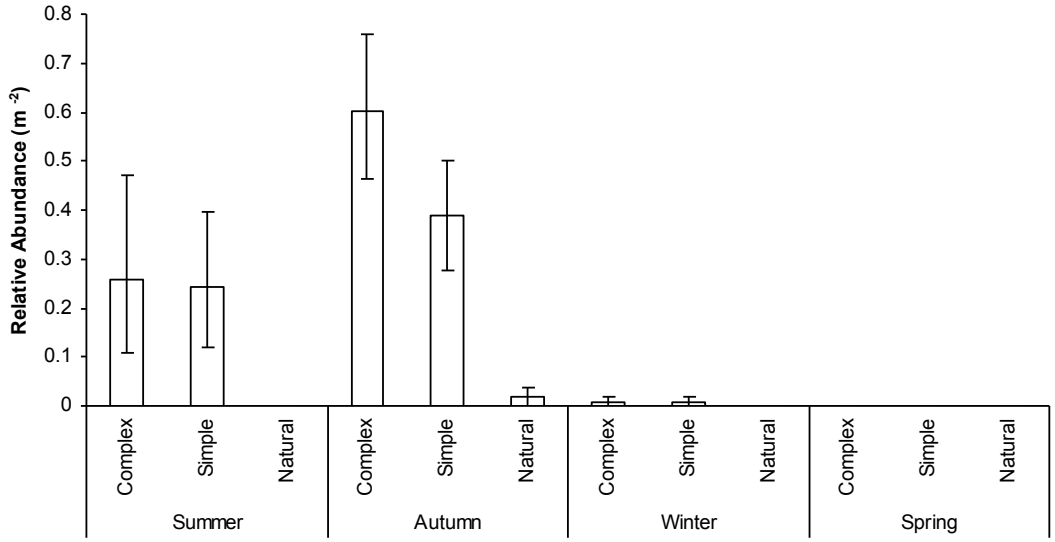


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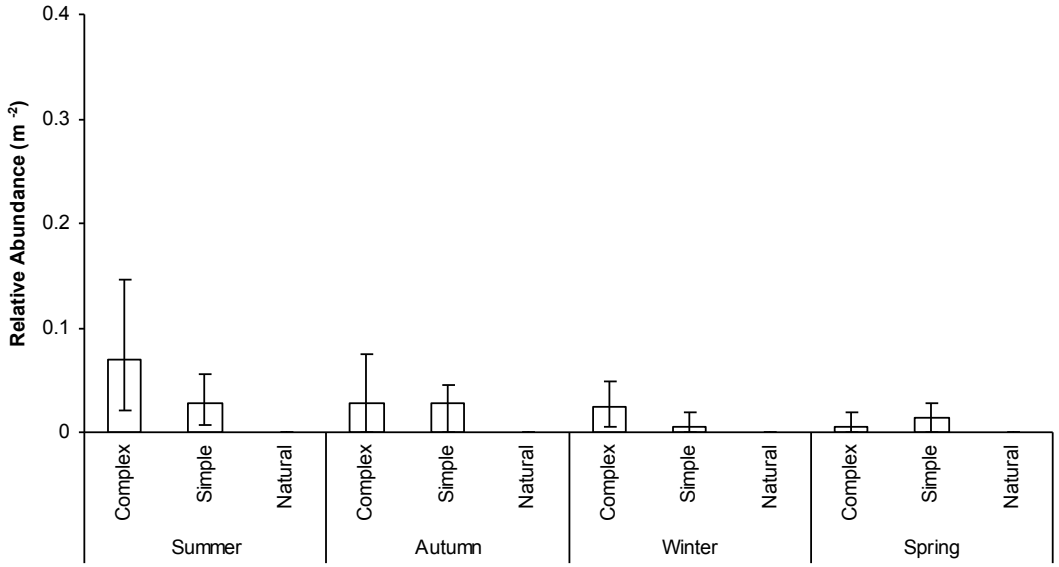
Figure 2 continued
(c)



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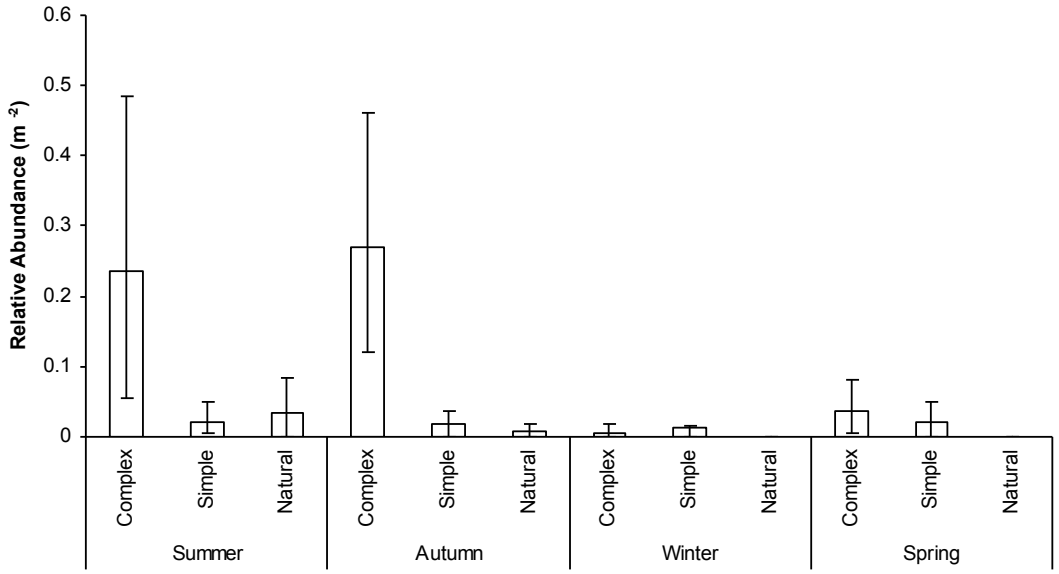
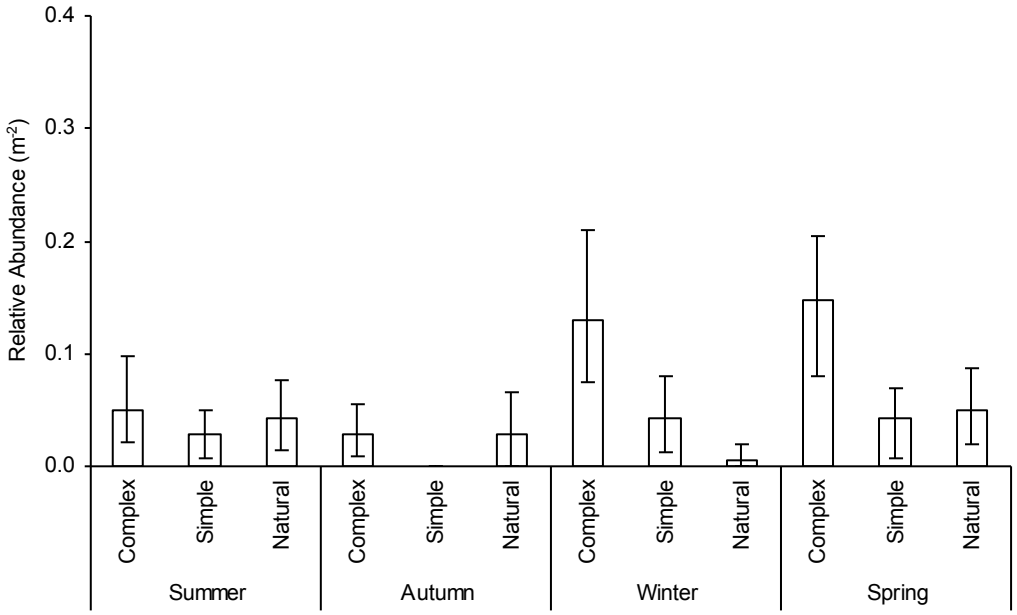


Figure 3. Mean relative abundance (per m^2) and 95% confidence intervals of the crustacean species (a) *Cancer pagurus* and (b) *Necora puber*, over the four seasonal regimes of summer, autumn, winter, and spring.

(a)



(b)

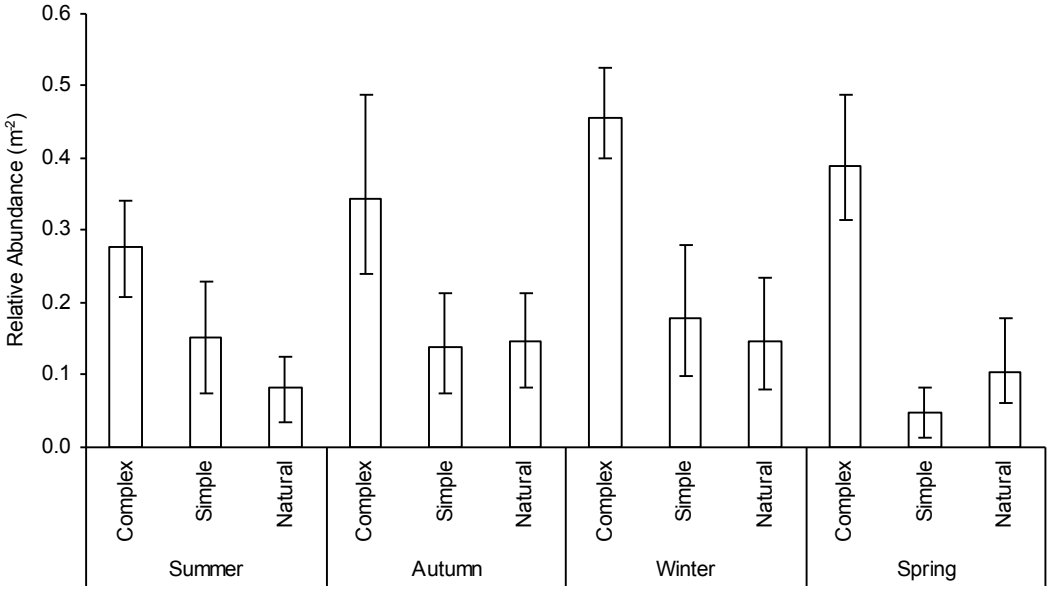
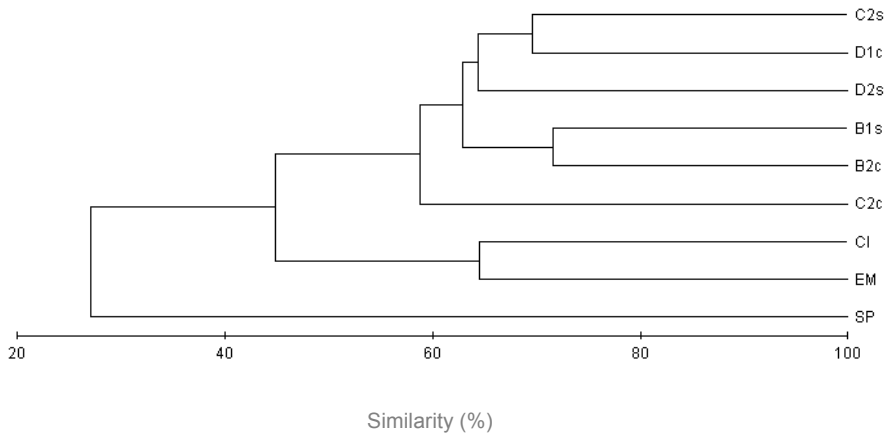


Figure 4. Cluster analysis calculated from the Bray–Curtis similarity index of faunal abundance at each site type during (a) summer, (b) autumn, (c) winter, and (d) spring. Complex artificial reefs are B2c, C2c, and D1c, simple artificial reefs are B1s, C2s, and D2s, and natural reefs are CI, EM, and SP.

(a)



(b)

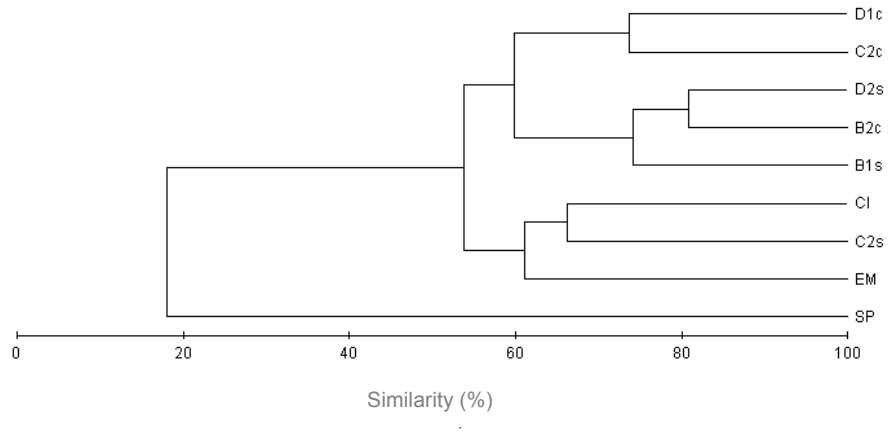


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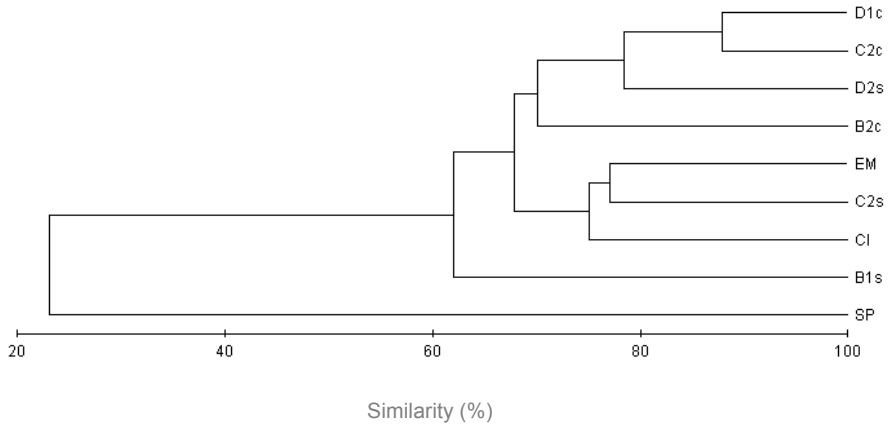
Figure 4 continued

(c)



(d)